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# THE DEVELOPMENT OF A SEA ANEMONE TENTACLE SPECIALIZED FOR AGGRESSION: MORPHOGENESIS AND REGRESSION OF THE CATCH TENTACLE OF *HALIPLANELLA LUCIAE* (CNIDARIA, ANTHOZOA)

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## ABSTRACT

Three intermediate catch tentacle morphs were observed in the sea anemone *Haliplanella luciae* during catch tentacle development.

Stage 1 catch tentacles, characterized by swollen bulb-like regions along their length, were histologically similar to feeding tentacles.

Stage 2 catch tentacles, which tapered normally along most of their length and then constricted near the tip, were characterized by the presence of feeding tentacle cnidae in the tentacle coelenteron as they were removed from developing catch tentacles. Numerous cnidoblasts appeared in stage 2 tentacles and then synchronously matured into small holotrich nematocysts, a cnida characteristic of mature catch tentacles.

Stage 3 catch tentacles were characterized by the appearance of many large holotrich nematocysts. Such tentacles appeared similar to mature catch tentacles with wide, opaque, blunt tips. However, stage 3 catch tentacles had fewer large holotrichs per total tentacle cross section than mature catch tentacles.

The numbers of large and small holotrich nematocysts decreased in regressing catch tentacles, which tapered to opaque, pointed tips. However, these cnidae did not move to the coelenteron as before but instead migrated to the epithelial surface. This migration suggested that they were externally expelled from the tentacles.

## INTRODUCTION

Two types of tentacles occur in certain acontiate sea anemones. One type, the typical feeding tentacle, is a translucent, slender structure that gently tapers from its base to a pointed tip. The second type of anemone tentacle, known as a catch tentacle, is opaque, about twice as wide as a feeding tentacle and blunt-tipped (Williams, 1975). Feeding tentacles usually move in concert in order to capture prey and bring them to the mouth. In contrast, catch tentacles move singly in a so-called "searching" behavior in which they can extend to three or four times their resting length, gently touch the substratum, retract and re-extend. This catch tentacle searching behavior was first described by Gosse in 1860 and later by Carlgren (1929), who also found that catch tentacles have a different cnidom (nematocyst complement) from feeding tentacles. Carlgren suspected that catch tentacles were specialized for feeding. Hence, he named the structures "*fangtentakeln*" (=catch tentacle). Hand (1955) observed that "materials" adhered to catch tentacles of the anemone *Metridium senile* and also noted that catch tentacles regressed into feeding tentacles in starved, isolated animals.

Williams (1975) was the first to recognize that catch tentacles were used in aggressive interactions among anemones. Food items that were touched to catch

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tentacles of the anemone *Haliplanella luciae* did not adhere to the tentacles, nor were the tentacles brought to the mouth. Williams cited unpublished observations by P. R. G. Tranter of the Plymouth Marine Laboratory that catch tentacles were used in intraspecific and interspecific aggressive interactions among the sea anemones *Cereus pedunculatus, Sagartia elegans,* and *Sagartia troglodytes.* Purcell (1977) fully described intraspecific aggressive behavior involving catch tentacles among different color morphs (non-clonemates) of *M. senile.* Following mutual feeding tentacle contact with a non-clonemate individual, a single catch tentacle elongates (as previously described for "searching" behavior). The elongated catch tentacle moves toward the "opponent" and its tip attaches (upon contact) to the upper column or tentacles of the opponent. The catch tentacle breaks slightly behind the tentacle tip as it is withdrawn, thereby leaving the autotomized tentacle tip attached to the "victim." Severe necrosis develops in the victim at the site of the attached catch tentacle tip, occasionally leading to the death of the victim.

In other experiments, Purcell found that catch tentacles developed from preexisting feeding tentacles in *M. senile* when different color morphs (non-clonemates) were crowded into a small aquarium. Since Carlgren (1929) had reported that catch tentacles have a different cnidom from feeding tentacles, this meant that feeding tentacle cnidae must somehow be replaced by catch tentacle cnidae during catch tentacle development. Spirocysts are the dominant cnida in feeding tentacles while holotrich nematocysts are the dominant cnida in catch tentacles (Hand, 1955; Williams, 1975; Purcell, 1977). Purcell (1977) demonstrated that such a turnover takes place during catch tentacle development by counting cnidae from squashes of developing catch tentacles using light microscopy. However, the morphogenetic processes that accompany catch tentacle development remain poorly understood.

The present study describes for the first time the morphogenetic processes involved in catch tentacle development and catch tentacle regression in the sea anemone *Haliplanella luciae.*

## MATERIALS AND METHODS

### *Animal collection and maintenance*

Two different clones of the sea anemone *Haliplanella luciae* were removed from rocks or small oyster clumps near the Florida State University Marine Laboratory, Turkey Point, Florida. A third *H. luciae* clone was collected by L. L. Minasian at the mouth of the Indian River in Delaware. Monoclonal *H. luciae* stock cultures were established following frequent fission events, beginning with isolated individuals of each *H. luciae* clone. Stock culture anemones were kept in culture dishes filled with natural sea water (28–30‰), which was changed daily and held at 17–19°C. The sea anemones were fed to repletion twice weekly with freshly hatched *Artemia* nauplii according to the methods of Minasian and Mariscal (1979).

Specimens of the sea anemone *Diadumene gracillima* (which can have catch tentacles) were collected from oyster clumps near the FSU Marine Lab. Unlike *H. luciae, D. gracillima* seldom reproduces asexually. Thus, experimental *D. gracillima* were not monoclonal. *Diadumene gracillima* was maintained in culture dishes filled with sea water by the methods described above for *H. luciae* stock cultures.

### *Induced catch tentacle development*

Three different biclonal, intraspecific cultures were established using the three *H. luciae* clones. Forty-eight organisms, twenty-four of each clone, were placed in

70 mm diameter culture dishes filled with sea water to a height of 10 mm (40 ml) in order to crowd the anemones and insure frequent tentacle contacts throughout the culture. In addition, a single interspecific anemone culture was established using twenty-four monoclonal *H. luciae* mixed with an equal number of *D. gracillima* in a culture dish filled with 40 ml of sea water. In order to control against possible effects of crowding on catch tentacle development, a control culture of forty-eight monoclonal *H. luciae* was established in a culture dish as before.

The procedures described above were intended to stimulate the development of catch tentacles in *H. luciae*. Anemone cultures were screened at approximately one-week intervals for developing catch tentacles, mature catch tentacles, and regressing catch tentacles.

### *Histology*

Specimens were anesthetized in their culture dishes using a one-to-one solution of 7.5% MgCl and sea water. All tentacles were fully relaxed in length. However, catch tentacle developmental stages characterized by constrictions in diameter (as described below) held their typical shape in the anaesthetic and throughout subsequent tissue processing. Developing catch tentacles and regressing catch tentacles were removed from the experimental animals at the interface of the tentacle base and oral disc using fine forceps, drawn into disposable pipettes and dropped into 100% formalin. For small pieces of tissue (*e.g.* anemone tentacles), it was discovered that 100% formalin gave superior results to other fixatives. Mature catch tentacles were removed from freshly-collected animals or from anemones held in long-standing laboratory cultures, then fixed using the technique described above. Following a four-hour fixation, the tissue was washed twice in distilled water, dehydrated in a graded ethanol series, cleared with toluene, and embedded in Paraplast Plus. Ten-micrometer cross sections were mounted and stained in azure a, eosin b for forty minutes after Lillie (1965), then viewed through a Nikon compound microscope using Nikon 15× oculars and a Nikon 100× plan, oil immersion objective lens. The three distal-most tentacle sections having gastrodermal tissue (to avoid counting tentacle tip shavings) were observed and their cnidae were grouped into three categories as follows.

1. Mature cnidae. All "mature" nematocysts (deep blue in azure a, eosin b) were identified by capsule morphology after Mariscal (1974). Mature spirocysts stained dark red in azure a, eosin b and were conspicuous by their color.
2. Cnidoblasts. Since this term is often used incorrectly, it should be pointed out that we use the term "cnidoblast" to refer to the developmental stages of cnidae only and not to the mature structures. Cnidoblasts stained pink in azure a, eosin b.
3. Gastrodermal cnidae. These are mature cnidae that are located in the gastrodermis or free in the coelenteron at the tentacle tip.

The average number of cnidae of the above categories was calculated from three sections per tentacle and compared for each of the following tentacle types: feeding tentacles, developing catch tentacles, mature catch tentacles, and regressing catch tentacles.

Initial examinations showed that the tentacle section cnidom (nematocyst complement) could differ among the tentacle types in (1) the total number of cnidae per section (*i.e.*, the "cnidom size") and/or in (2) the percentages of various cnida types in relation to the tentacle section cnidom. Therefore, these two parameters were studied in detail and are described below.

### *Cnidom size*

The cnidom size is a measure of the number of cnidae per tentacle tip cross section. In this study, the feeding tentacle cross section cnidom (of 114.7 cnidae, n = 6) was used as a standard "unit cnidom." The cnidom size for a given tentacle type was calculated by dividing the average number of cnidae per tentacle cross section by the average number of cnidae (114.7) per feeding tentacle cross section. Thus, tentacle types with fewer than 114.7 cnidae per tentacle section had a corresponding cnidom size that was smaller than 1.00 unit cnidom, while tentacle types with more than 114.7 cnidae per section had a somewhat larger cnidom size than 1.00 unit cnidom.

Catch tentacle morphogenesis and regression involve substantial tentacle growth and degrowth (*i.e.*, a decrease in tentacle diameter) and thus result in significant changes in tentacle shape. Such changes occur in addition to changes in the tentacle cnidom. Methods of counting cnidae per unit circumference or area are not suited for use in this study since tentacle circumference (or area) can change along with the tentacle cnidom and thereby mask changes in the cnidom. The method of counting all of the cnidae per cross section for each tentacle type avoids such complications caused by tentacle growth (or degrowth) processes.

### *Cnida percentage*

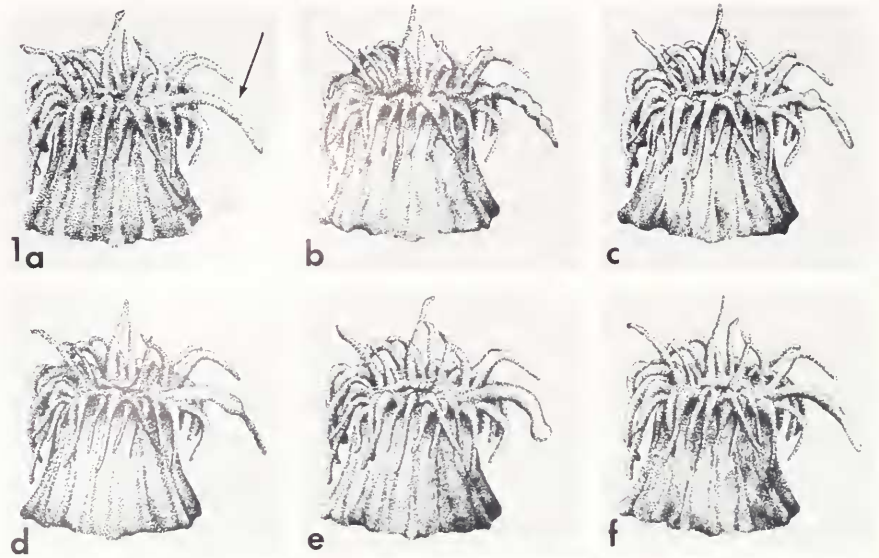
So that changes in the tentacle cnidom that might occur without affecting cnidom size (*e.g.*, a balanced addition and deletion of different cnida types) could be detected, the percentage of each cnida type was determined in relation to the total cross section cnidom for each type of tentacle. For example, as described below, feeding tentacles had an average of 114.7 total cnidae per tentacle section. Of these 114.7 cnidae, 65.8 (or 57.3%) were spirocysts.

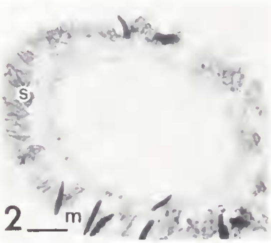
## RESULTS

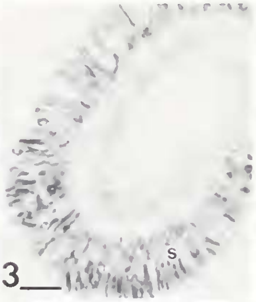
Three distinct developing catch tentacle morphs were observed in *H. luciae* held in intraspecific and interspecific anemone cultures. These were labeled "stage 1," "stage 2," and "stage 3," according to their order of appearance in anemones during catch tentacle development. There was no appreciable histological difference between developing catch tentacles of *H. luciae* held in interspecific cultures and those of *H. luciae* held in intraspecific cultures, although the former developed more rapidly (Watson and Mariscal, in prep.).

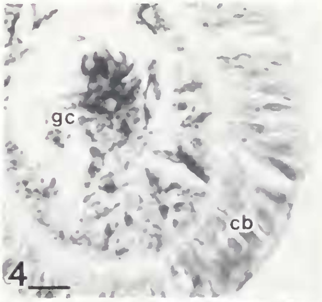
### *Tentacle morphs*

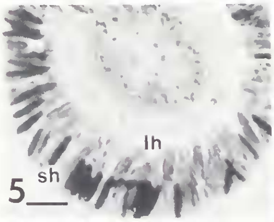
A feeding tentacle gently tapers from its base to a pointed tip (Fig. 1a). On the other hand, the stage 1 intermediate catch tentacle has temporary bulb-like regions (one to several) that stand out along its length for a few hours at a time. The multiple-bulb morph is shown in Figure 1b and the single-bulb morph in Figure 1c. The stage 2 intermediate catch tentacle tapers normally along its length and then constricts sharply near the tip for a few hours at a time (Fig. 1d). The stage 3 intermediate catch tentacle is a permanent structure that appears identical to a fully mature catch tentacle. It is blunt-tipped, wider than adjacent feeding tentacles, and opaque (Fig. 1e). A regressing catch tentacle gently tapers to a pointed tip, like a feeding tentacle, but retains opacity (reminiscent of a catch tentacle) in distal tentacle regions (Fig. 1f).

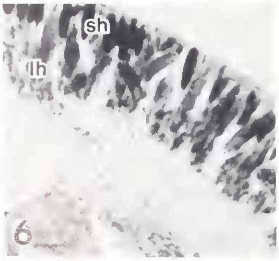


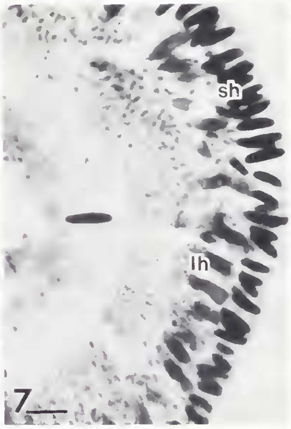












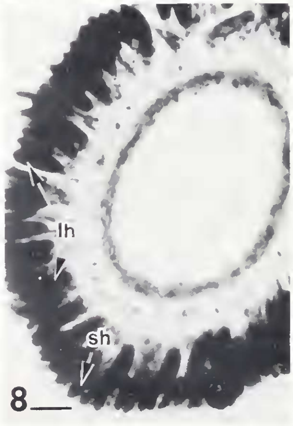


FIGURE 1. Illustration of catch tentacle developmental stages: (a) innercycle feeding tentacle (arrow), (b) stage 1 intermediate catch tentacle, "multiple-bulb" morph, (c) stage 1 intermediate catch tentacle, "single-bulb" morph, (d) stage 2 intermediate catch tentacle, (e) stage 3 intermediate catch tentacle (=mature catch tentacle), (f) regressing catch tentacle.

FIGURE 2. Photomicrograph of a feeding tentacle tip (formalin fixed and stained in azure a, eosin b). Note translucent spirocysts (s) and opaque microbasic p-mastigophores (m). Scale bar is 10 $\mu$m.

FIGURE 3. Photomicrograph of a stage 1 intermediate catch tentacle tip in cross section dominated by spirocysts (s). Scale bar is 10 $\mu$m.

### *Tentacle tip histology*

#### *Feeding tentacle*

Feeding tentacles were dominated by spirocysts, followed by microbasic p-mastigophore nematocysts (Fig. 2). Occasional basitrich nematocysts also were present in these sections. The numerous mature cnidae were distributed at the epithelial surface while the occasional cnidoblasts were beneath them. Gastrodermal cnidae were rare in feeding tentacles.

#### *Stage 1 intermediate catch tentacle*

Stage 1 tentacles (histologically similar to feeding tentacles) were dominated by spirocysts, followed by microbasic p-mastigophores, and basitrichs (Fig. 3). Occasional cnidoblasts were observed in these tentacles along with a few gastrodermal cnidae.

#### *Stage 2 intermediate catch tentacle*

Stage 2 tentacles, although morphologically identical, varied histologically (Figs. 4, 5). Therefore, the tentacles were grouped into three characteristic substages (a, b, and c), which are described below.

Stage 2a tentacles, like feeding and stage 1 tentacles, were dominated by spirocysts, microbasic p-mastigophores, and basitrichs. However, the numbers of these cnidae were greatly reduced from those in feeding and stage 1 tentacles. Cnidoblasts were rare in these tentacles, but gastrodermal cnidae were more common than in feeding tentacles and stage 1 tentacles. Since 2a tentacles were qualitatively similar to stage 1 and feeding tentacles, a 2a tentacle photomicrograph is not shown.

Stage 2b tentacles were characterized by numerous cnidoblasts in their epithelium along with a few typical catch tentacle cnidae (small holotrich and large holotrich nematocysts), which appeared for the first time in this stage (Fig. 4). Feeding tentacle cnidae (spirocysts, microbasic p-mastigophores, and basitrichs) were rare in stage 2b tentacles. This is in contrast with feeding, stage 1, and stage 2a tentacles, in which feeding tentacle cnidae dominated the tentacle cnidom. However, gastrodermal cnidae were as common as in stage 2a tentacles.

Stage 2c intermediate catch tentacles were dominated by mature catch tentacle cnidae (small holotrich nematocysts), but unlike stage 2b tentacles, 2c tentacles

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FIGURE 4. Photomicrograph of a stage 2b intermediate catch tentacle tip seen in cross section. Note the numerous cnidoblasts (cb) in the tentacle epithelium and gastrodermal cnidae (gc) free in the tentacle coelenteron. Scale bar is 10 $\mu$m.

FIGURE 5. Photomicrograph of a stage 2c intermediate catch tentacle tip seen in cross section. Small holotrich nematocysts (sh) are distributed at the epithelial surface and large holotrichs (lh) are recessed from the epithelial surface. The tentacle is collapsed about its coelenteron. Scale bar is 10 $\mu$m.

FIGURE 6. Photomicrograph of a stage 3 intermediate catch tentacle tip seen in cross section. Small holotrichs (sh) line the epithelial surface and large holotrichs (lh) are recessed from the epithelial surface. Scale bar is 10 $\mu$m.

FIGURE 7. Photomicrograph of a mature catch tentacle tip seen in cross section. Note the numerous small holotrichs (sh) at the epithelial surface and large holotrichs (lh) recessed from the epithelial surface. Scale bar is 10 $\mu$m.

FIGURE 8. Photomicrograph of a regressing catch tentacle tip seen in cross section. Large holotrichs (lh) line the epithelial surface alongside small holotrichs (sh). Scale bar is 10 $\mu$m.

Note that Figures 2 through 8 are shown at the same magnification, indicating actual differences in tentacle size.

lacked cnidoblasts (Fig. 5). Feeding tentacle cnidae were rare in the 2c tentacle epithelium, but gastrodermal cnidae were often as common as in 2a and 2b tentacles.

### *Stage 3 intermediate catch tentacle*

Stage 3 catch tentacles had many more cnidae than any of the types of tentacles discussed above (Fig. 6), because of the appearance of additional small holotrichs in these tentacles along with many large holotrichs (which had been extremely rare in stage 2 catch tentacles). The small holotrichs were distributed at the epithelial surface and the large holotrichs were recessed from the epithelial surface beneath the small holotrich cnidocytes. Feeding tentacle cnidae were extremely rare in stage 3 tentacles, as were gastrodermal cnidae. Cnidoblasts were absent from this stage. Note that the diameter of the stage 3 catch tentacle is much larger than that of the previous developmental stage (*i.e.*, significant growth has occurred).

### *Mature catch tentacle*

Mature catch tentacles, like stage 3 catch tentacles, were characterized by numerous small holotrichs at the epithelial surface, followed by large holotrichs recessed from the epithelial surface (Fig. 7). However, feeding tentacle cnidae (rare in stage 3 tentacles) were absent from mature catch tentacle tips. Likewise, cnidoblasts were absent, and gastrodermal cnidae were rare in mature catch tentacles.

### *Regressing catch tentacle*

Even though regressing catch tentacles had far fewer cnidae in their epithelium than mature catch tentacles, numerous small holotrich and large holotrich nematocysts were present in these tentacles (Fig. 8). Note that large holotrichs were distributed alongside small holotrichs at the epithelial surface in regressing catch tentacles. This holotrich distribution is in contrast with stage 3 and mature catch tentacles, in which large holotrichs were recessed from the epithelial surface. In addition, occasional feeding tentacle cnidae were observed in the tips of regressing catch tentacles, whereas none had been present in mature catch tentacle tips. Cnidoblasts were absent and gastrodermal cnidae were rare. Note that the diameter of the tentacle has decreased dramatically (*i.e.*, degrowth has occurred).

## *Quantitative histology*

### *Feeding tentacle*

Feeding tentacles had an average of 114.7 cnidae per tentacle tip cross section (equivalent to a 1.00 unit cnidom, n = 6). Of these 114.7 cnidae, 57.3% were spirocysts, 26.5% were microbasic p-mastigophore nematocysts, 5.2% were basitrich nematocysts, 2.2% were gastrodermal cnidae, and 9.8% were cnidoblasts (Fig. 9). The *H. luciae* feeding tentacle complement of spirocysts (at 57%) of the tentacle cnidom is lower than those reported by Purcell (1977) for *Metridium senile* (at 80%) and Schmidt (1982) for *Anemonia sulcata* (at 68%) but is in general agreement with the findings of Bigger (1982) for four anemone species. In this study, Bigger reported that the spirocyst complement ranged from 49% to 79% of the feeding tentacle cnidom.

### *Stage 1 intermediate catch tentacle*

Stage 1 intermediate catch tentacles had slightly fewer cnidae than feeding tentacles with an average of 104.6 cnidae per tentacle cross section (104.6/114.7 = a

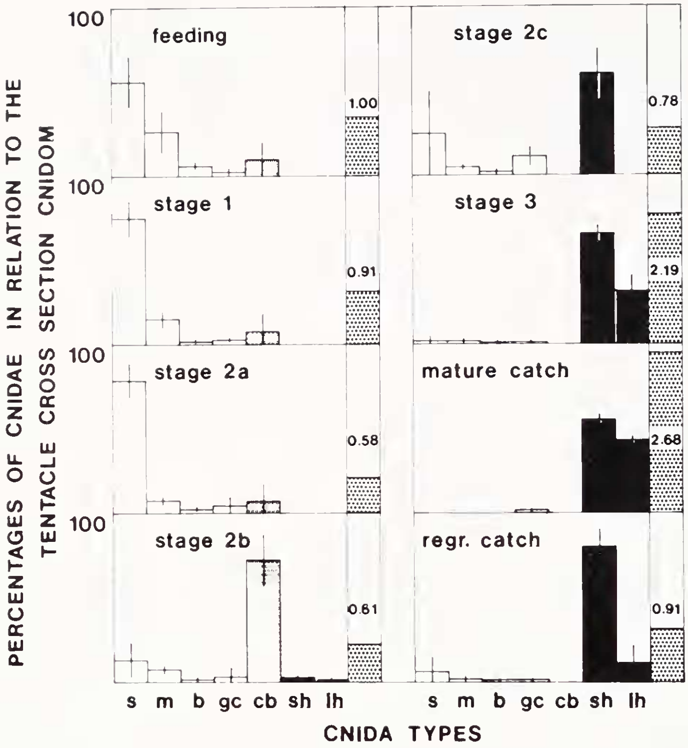

FIGURE 9. Percentages of cnidae in relation to the tentacle cross section cnidom. The percentage of each cnida type (listed below) was determined in relation to the tentacle cross section cnidom. These values were averaged for tentacles of the same type and the resultant values are shown in bars drawn to scale ± standard deviation (depicted as error bars). Feeding tentacle cnida types (white bars): spirocysts (s), microbasic p-mastigophores (m), basitrichs (b), gastrodermal cnidae (gc). Cnidoblasts (stippled bars, open circles ) (cb). Catch tentacle cnida types (black bars): small holotrichs (sh), large holotrichs (lh).

In the inset at right (stippled bars, closed circles), the cnidom size is given for each type of tentacle (drawn to scale) as a function of the average total number of cnidae per feeding tentacle cross section (the unit cnidom).

0.91 unit cnidom, n = 3). The stage 1 intermediate catch tentacle cnidom was divided into 76.3% spirocysts, 14.3% microbasic p-mastigophores, 0.7% basitrichs, 1.7% gastrodermal cnidae, and 7.0% cnidoblasts (Fig. 9).

### *Stage 2 intermediate catch tentacle*

Stage 2a tentacles were marked by a sharp decrease in the number of cnidae per tentacle section from the 0.91 unit cnidom of stage 1 tentacles to a 0.58 unit cnidom in stage 2a tentacles (n = 2). This "smaller" tentacle cnidom was made up of 78.3% spirocysts, 7.7% microbasic p-mastigophores, 2.7% basitrichs, 4.7% gastrodermal cnidae, and 6.7% cnidoblasts (Fig. 9). Note that all of the types of cnidae that occurred in feeding and stage 1 tentacles were present in stage 2a tentacles in percentages that were similar to those observed for stage 1 tentacles. However, since there was a sharp decrease in the cnidom size from 0.91 to 0.58, the decrease in numbers of cnidae was evenly distributed among all of the cnida types.

Stage 2b tentacles had a cross section cnidom (a 0.61 unit cnidom, n = 2) that was slightly greater than the 2a tentacle cnidom. The 2b tentacle cross section cnidom was composed of 13.0% spirocysts, 6.5% microbasic p-mastigophores, 0.5% basitrichs, 3.0% gastrodermal cnidae, 73.0% cnidoblasts, 3.5% small holotrichs, and 0.5% large holotrichs (Fig. 9). Thus, the percentages of feeding tentacle cnidae in general, and spirocysts in particular, decreased in 2b tentacles, while the percentage of cnidoblasts increased dramatically. However, the cnidom size of 0.61 unit cnidom was about the same as for the 2a tentacles. In addition, catch tentacle cnidae (small and large holotrichs) appeared for the first time in the epithelium of 2b tentacles.

Stage 2c tentacles had a cross section cnidom that was somewhat larger at a 0.78 unit cnidom (n = 2) than the previous two substages. The 2c intermediate catch tentacle cnidom consisted of 25.5% spirocysts, 4.5% microbasic p-mastigophores, 1.0% basitrichs, 11.0% gastrodermal cnidae, 0.0% cnidoblasts, 58.0% small holotrichs, and 0.0% large holotrichs (Fig. 9). Hence, 2c tentacles were characterized by the sharp decrease of cnidoblasts (to zero) along with a sharp increase in the percentage of small holotrichs. However, the percentage of large holotrichs did not increase in 2c tentacles, and the percentages of feeding tentacle cnidae remained low.

### *Stage 3 intermediate catch tentacle*

The cnidom size of stage 3 catch tentacles (at a 2.19 unit cnidom, n = 7) was 2.8 times larger than that of stage 2c catch tentacles. The stage 3 catch tentacle cnidom was made up of 1.7% spirocysts, 0.9% microbasic p-mastigophores, 0.1% basitrichs, 0.3% gastrodermal cnidae, 0.0% cnidoblasts, 65.8% small holotrichs, and 31.0% large holotrichs (Fig. 9). Thus, this "large" tentacle cnidom was dominated by catch tentacle cnidae while each of the feeding tentacle cnida types (spirocysts, microbasic p-mastigophores, and basitrichs) decreased to less than 2.0% of the cnidom. These data are in general agreement with those of Purcell (1977) for newly developed catch tentacles (=stage 3 catch tentacles) of *M. senile.*

### *Mature catch tentacle*

Mature catch tentacles had a larger cnidom size (at a 2.68 unit cnidom, n = 6) than stage 3 catch tentacles (at 2.19). The mature catch tentacle cross section cnidom comprised 0.0% spirocysts, 0.0% microbasic p-mastigophores, 0.0% basitrichs, 0.2% gastrodermal cnidae, 0.0% cnidoblasts, 56.2% small holotrichs, and 43.7% large holotrichs (Fig. 9). Note that the percentage of large holotrichs increased and the percentage of small holotrichs decreased in mature catch tentacles from those in stage 3 catch tentacles. Thus, the increase in cnidom size was caused by the addition of large holotrichs, while the number of small holotrichs stayed constant. This pattern is also shown by a comparison of the average raw numbers of these cnidae in mature catch tentacles versus stage 3 catch tentacles. An average of 170.2 small holotrichs and 137.5 large holotrichs were present in mature catch tentacles (per tentacle tip section), while 163.7 small holotrichs and 82.6 large holotrichs occurred in stage 3 catch tentacles.

### *Regressing catch tentacle*

The cnidom size of regressing catch tentacles (at a 0.91 unit cnidom, n = 3) was about one-third that of mature catch tentacles. The regressing catch tentacle cnidom was made up of 6.0% spirocysts, 2.0% microbasic p-mastigophores, 0.3% basitrichs, 1.0% gastrodermal cnidae, 0.0% cnidoblasts, 80.3% small holotrichs, and 10.3% large holotrichs (Fig. 9). Therefore, at this point in catch tentacle regression, catch tentacle cnidae still dominated the cnidom even though their numbers were reduced by two-thirds. Notice that feeding tentacle cnidae had appeared in these tentacles in their "normal" relative proportions (*i.e.*, with spirocysts more numerous than microbasic p-mastigophores, which were more numerous than basitrichs). It is also important to point out that the percentage of gastrodermal cnidae was low (at 1.0%) in regressing catch tentacles. The significance of this "small" gastrodermal cnidae complement will be discussed later.

## DISCUSSION

### *Catch tentacle development*

#### *Stage 1 intermediate catch tentacle*

The multiple-bulb and single-bulb stage 1 tentacle morphs are each consistently observed in tentacles that develop into catch tentacles (the multiple-bulb morph appears first). Although nothing is known about the role of these bulbs in anthozoans, similar phenomena have been reported in hydrozoans, where they have been correlated with certain growth processes such as body lengthening and broadening. Beloussov (1973) studied "growth pulse" phenomena in stolon and hydranth growth in some hydrozoans, including *Dyamena pulima.* He thought that growth pulses arose from antagonistic myoepithelial cell movements between the hydrotheca and connective tissue layer that allowed the myoepithelial cell layer to extend beyond the hydrotheca, and thereby caused the stolon to elongate and the stolon tip to broaden.

Campbell (1980) recently proposed a model that related growth pulse phenomena to morphogenetic changes along *Hydra* stalks. Campbell suggested that myoepithelial cells stretch to their maximum extension by creeping of their cell processes in opposite directions. Continued creeping of these myoepithelial cell processes compresses the connective tissue layer. Hydrostatic pressure is generated in the gastric cavity that counteracts this compression of connective tissue and thereby deforms the myoepithelial cell layer. As a result, myoepithelial cells shift with respect to one another, and thus morphogenetic changes result. Campbell postulated that such processes are also involved in *Hydra* tentacle growth and development.

The resemblance borne by *H. luciae* stage 1 tentacle "pulses" (=bulbs) to known hydrozoan "growth pulses" suggests that these anthozoan tentacles might be involved in processes that account for tentacle widening and tentacle tip broadening during catch tentacle development, since catch tentacles are about twice as wide as feeding tentacles and blunt-tipped, whereas feeding tentacles are thin and have pointed tips.

This idea is supported by our observation of occasional multiple-bulb tentacle morphs in small tentacles in the outermost cycles of tentacle in some animals and also in small, newly-formed tentacles over fission scars. Thus tentacle "bulbs" similar to those in stage 1 intermediate catch tentacles occur in anemone tentacles that are almost certainly undergoing growth and development. Therefore, outer cycle "bulbed" tentacles are probably involved in general growth processes while inner cycle "bulbed" tentacles (which are already fully formed) are probably involved in the morphogenetic conversion of feeding tentacles into catch tentacles. Catch tentacles only develop in inner cycles of tentacles on the oral disc (Williams, 1975).

Inasmuch as the histology of stage 1 tentacle tips was similar to that of feeding tentacle tips, it is clear that stage 1 tentacles are not involved in cnidae turnover. This occurs in stage 2 tentacles and is discussed below.

### *Stage 2 intermediate catch tentacle*

Feeding tentacle cnidae (spirocysts, microbasic p-mastigophores, and basitrichs) migrate (or are phagocytized by granulocytes and then transported) from the epithelium to the coelenteron in stage 2 tentacles. Hence, feeding tentacle cnidae are gradually removed from developing catch tentacles, but their fate beyond this point is not known. Perhaps these so-called "gastrodermal cnidae" are inserted into other anemone tissues (*e.g.*, into other feeding tentacles) or somehow eliminated and/or expelled from the anemone. The "removal" of feeding tentacle cnidae is followed by the appearance of numerous cnidoblasts in the epithelium. It is possible that interstitial cells (stem cells) migrate into stage 2 tentacles and then differentiate into cnidoblasts or, alternatively, that local stem cells (already present) proliferate and then differentiate into cnidoblasts. Since stage 2 tentacles were filled with numerous small holotrich cnidoblasts, or with numerous small holotrich cnidocytes, and not a mixture of the two, it is clear that the cnidoblasts synchronously mature into catch tentacle cnidocytes (the mature cell containing the mature structures).

### *Stage 3 intermediate catch tentacle*

Large holotrichs are usually absent from the tips of stage 2 intermediate catch tentacles (which can contain numerous small holotrichs), and first appear in the tips of stage 3 intermediate catch tentacles. However, stage 3 catch tentacles consistently have fewer large holotrichs in their epithelia than mature catch tentacles (although stage 3 catch tentacles have about as many small holotrichs as mature catch tentacles). Thus, the appearance of large holotrichs occurs much later during catch tentacle development than the appearance of small holotrichs. These data suggest that the differentiation of interstitial cells into large holotrich cnidocytes is regulated so that the interstitial cells do not form into large holotrich cnidocytes until after many small holotrich cnidocytes have been produced and line the epithelial surface (*i.e.*, late in catch tentacle development).

Since stage 3 catch tentacles lack cnidoblasts at the tentacle tip, the source of the additional cnidae that are necessary for final catch tentacle maturation is unknown. Perhaps the pulse-like appearance of cnidoblasts and synchronous maturation into holotrich cnidocytes (observed in stage 2 tentacles) recurs throughout catch tentacle development. On the other hand, holotrichs might be produced in proximal tentacle regions and then transported through the tentacle coelenteron to be inserted into the distal tentacle epithelia. Another possible explanation is based on the fact that stage 3 catch tentacles, like mature catch tentacles, are functional, aggressive structures that autotomize their tentacle tips during normal functioning. Thus, this "deficiency" in the number of cnidae per tentacle section might be overcome by tissue renewal processes in the "new" catch tentacle tips following tentacle tip autotomy during aggression.

### *Mature catch tentacle*

Note that the percentages of small and large holotrichs (respectively) in relation to the cross section cnidom were nearly identical among the six mature catch tentacles used in this study (*i.e.*, the standard deviation was small—see Figure 9). Since the mature catch tentacle cnidom is made up almost entirely of small and large holotrichs, it is possible that the total number of large holotrich cnidocytes that differentiate from interstitial cells in the latter stages of catch tentacle development is related to the total number of small holotrich cnidocytes that were produced in "early" stages of catch tentacle development (*i.e.*, in a fixed ratio of 1.0 large holotrichs produced per 1.3 small holotrichs). However, since the distribution of the two types of holotrichs is spatially distinct, with small holotrichs lining the epithelial surface and large holotrichs occupying the space beneath them, this ratio of large to small holotrichs might simply reflect optimal densities of each cnida type independent of the other. Catch tentacles are particularly suited for demonstrating possible regulation of this type (or maximization of space utilization) because normal tissue depletion in catch tentacles includes tentacle tip autotomy (an intermittent, all-or-none phenomenon).

### *Catch tentacle regression*

The removal of catch tentacle cnidae (small and large holotrichs) from regressing catch tentacles is concurrent with the appearance of feeding tentacle cnidae. The holotrichs are not transported to the tentacle coelenteron (to become "gastrodermal cnidae") during catch tentacle regression, as feeding tentacle cnidae are during catch tentacle development. Instead, large holotrichs move from the middle epithelium to the epithelial surface alongside the small holotrichs, indicating that both types of holotrichs are probably expelled from these tentacles externally. The source of the mature feeding tentacle cnidae that appear in the tips of regressing catch tentacles is not yet known, since cnidoblasts were absent from the tips of the regressing catch tentacles used in this study.

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